AN INCOMPLETE PTEROSAUR SKULL FROM THE CRETACEOUS OF NORTH-CENTRAL QUEENSLAND, AUSTRALIA ¹

(With 6 figures)

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ABSTRACT: An incomplete pterosaur skull was found in the Albian marine Toolebuc Formation near Hughenden, Queensland, Australia. Although only the snout and part of the jaws are preserved, the specimen has two unique characters: posterior dentary teeth relatively large (approximately half the depth of the dentary) and posterior dentary and maxillary teeth relatively widely spaced (only 3 maxillary teeth between the last enlarged tooth and the nasopreorbital opening), and a unique combination of other characters. Thus, it is assigned to the new genus and species, *Mythunga camara* gen.nov., sp.nov., provisionally related to plesiomorphic pterodactyloids. The snout was apparently hollow with a boxlike internal structure, supporting the characterization of pterosaurs as 'optical illusions'. This specimen represents at least the second pterosaur taxon from Queensland.

Key words: Cretaceous. Australia. *Mythunga* gen.nov. Queensland. Albian. Archaeopterodactyloidea. Toolebuc Formation.

RESUMO: Um crânio incompleto de pterossauro do Cretáceo do centro-norte de Queensland, Austrália.

Um crânio incompleto de pterossauro foi encontrado em rochas do Albiano marinho da Formacão Toolebuc próximo a Hughenden, Queensland, Austrália. Apesar de apenas o focinho e mandíbulas incompletas estarem preservadas, o espécime possui duas características únicas: dentes mandibulares posteriores relativamente grandes (aproximadamente metade da altura da a mandíbula) e dentes maxilares e mandibulares posteriores posicionados relativamente distantes uns dos outros (apenas 3 dentes maxilares entre o mais posterior dos grandes dentes e a abertura nasoantorbital) e uma combinação única de outros caracteres. Então, é aqui determinado um novo gênero e espécie, *Mythunga camara*, provisoriamente relacionado aos pterodactilóides plesiomórficos. O focinho era aparentemente oco com uma estrutura interna compartimentada, suportando a caracterização de pterossauros como "ilusões de ótica". Esse espécime representa ao menos o segundo táxon de pterossauro de Queensland.

Palavras-chave: Cretáceo. Australia. *Mythunga* gen.nov. Queensland. Albiano. Archaeopterodactyloidea. Formação Toolebuc.

INTRODUCTION

The anterior portion of a pterosaur skull was discovered in April 1991 by Phillip Gilmore on Dunluce Station, near Hughenden, north-central Queensland. It was embedded in a calcareous nodule from the Toolebuc Formation. This is the first evidence of a pterosaur from north-central Queensland, although this unit has yielded pterosaur material near Boulia, some 500km to the southwest (Fig.1). Broken and dissociated pieces of ichthyosaurs, as well as ammonites and other mollusks were observed in the area where the snout was recovered. This specimen is the most complete pterosaurian cranial material from Australasia. Sporadic occurrences of other pterosaur material have been reported in Australasia: in addition to the described material from Boulia (Molnar & Thulborn, 1980; Molnar, 1987), a pubis (QM F27104) and flight metacarpal (NMV P197962) indicate substantially larger pterosaurs than previously known. The Lower Cretaceous of Victoria (reported by Rich & Rich, 1989), and the Upper Cretaceous of Western Australia (Bennett & Long, 1991) and New Zealand (WIFFEN & Molnar, 1988; Molnar & WIFFEN, 1994) have also produced pterosaurs.

Collection designations - AMNH (American Museum of Natural History, New York City); CAMSM (Sedgwick Museum, Cambridge); NMV (Museum of Victoria, Melbourne); QM (Queensland Museum, Brisbane).

¹ Submitted on September 14, 2006. Accepted on October 25, 2007.

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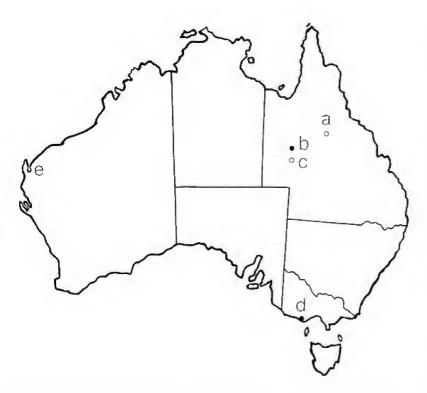


Fig.1- Australian pterosaur localities: (a) Dunluce Station, Albian (*Mythunga camara* sp.nov.); (b) Warra Station, Albian (aff. *Lonchodectes* sp., ?Anhangueridae & NMV P197962); (c) Elizabeth Springs, Albian (QM F27104); (d) Dinosaur Cove, Aptian-Albian (RICH & RICH, 1989); (e) Giralia Range, Maastrichtian (BENNETT & LONG, 1991).

RESULTS

Systematic Palaeontology

Pterosauria Kaup, 1834 Pterodactyloidea Plieninger, 1901 Archaeopterodactyloidea Kellner, 1996

Genus Mythunga gen.nov.

Diagnosis – As for type species, below.

Type species – Mythunga camara sp. nov.

Etymology – From 'Mythunga', referring to a star and a hunter of the skies in an unspecified western Queensland aboriginal dialect (DUNCAN-KEMP, 1968).

Mythunga camara sp.nov.

Diagnosis – Pterodactyloid with straight, slender snout; upper and lower teeth conical, slightly recurved, widely spaced, and lower teeth uniformly decreasing in height posteriorly; upper tooth row extends well back – at least three teeth in both jaws under anterior part of nasopreorbital opening; three maxillary teeth between last enlarged tooth and anterior edge of nasopreorbital fenestra (a); nasopreorbital opening relatively close to posterior margin of symphysis (only two upper teeth between them); nasopreorbital opening anteriorly rounded, not acutely angled; jaw margins strongly corrugated; upper jaw margin straight; anterior teeth enlarged; remainder of teeth relatively large, height of posterior dentary crowns approximately half of jaw depth (a); dentary symphysis narrow. Autapomorphies marked a.

Etymology – From *kamara* (Gr.), chamber, referring to the hollow, boxlike structure of the snout.

Holotype – QM F18896, an incomplete snout and adherent mandible.

Locality – Toolebuc Formation (Late Albian: Exon & SENIOR, 1976); Dunluce Station, west of Hughenden, north-central Queensland (Fig.1).

PRESERVATION

One-third to one-half of the skull and jaws are preserved (Figs.2-3). The snout and corresponding portions of the mandible, incomplete anteriorly, are preserved back to the anterior part of the nasopreorbital fenestra. The right side has been sheared upwards slightly relative to the left. This resulted in both mandibular rami being visible on the right side of the nodule, whilst only the left is visible on the left. The close interlocking of the upper and lower teeth indicates that the mandible probably remains in the position it held during life.

The snout has been mildly crushed, but there is no indication of plastic deformation. The lower part of the snout on the left has suffered longitudinal fractures, evincing no displacement, that form relatively smooth curves. These bound a depressed region that extends anteriorly at least to the level of the second preserved dentary tooth. The dorsal portion of the snout has been lost, more so on the right than the left. An unknown amount, but likely little (see below), has also been lost from the tip of the snout. The preserved part of the snout is 21.5cm long, and 7.1cm deep at its posterior break. The dorsal portion and anterior extremity of the nasopreorbital opening are preserved, but ventrally the margin is somewhat broken. Fragments of skull or mandible lay within the nasopreorbital fenestra on the left side, and between the mandibular rami on the right. The mandible is 4cm deep as preserved, and the left ramus shows a longitudinal break, similar to those described for the snout, apparently due to crushing. The ventral margin of the right ramus and anterior portion of the left are eroded (Fig.3).

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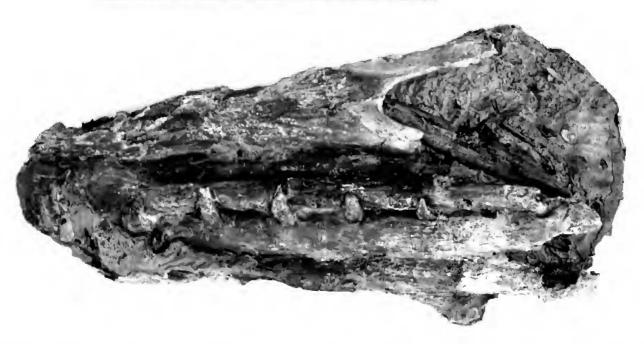


Fig.2- *Mythunga camara* gen.nov, sp.nov. Hughenden region, Queensland, Australia; Toolebuc Formation, Early Cretaceous. Holotype (QM F18896). Snout and mandible, left ventro-lateral view. This is a slightly different perspective from that of figure 4. Scale in mm.

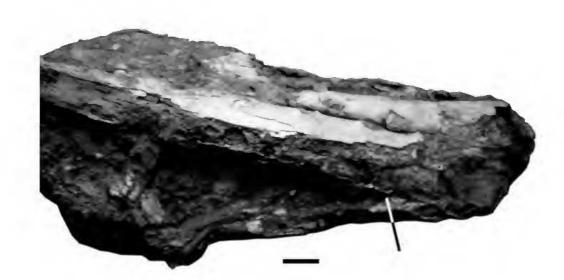


Fig.3- Mythunga camara sp.nov. (QM F18896), right lateral view. Bar indicates posterior margin of symphysis. Scale bar = 2cm.

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The teeth are fractured, in some cases the enamel is buckled near the base, and the tips (except for the last) are missing, so their form is not entirely clear. All of the left upper teeth but the anteriormost two have been lost, however all save the posteriormost two left mandibular teeth are present. The missing teeth had slipped out of their alveoli, presumably before burial. By contrast all of the crowns, both upper and lower, on the right side have been broken off. Since the teeth that slipped from their sockets were presumably exposed, their absence on the left suggests that the skull came to rest on its right side, and may have been exposed for some time before burial. However, the bones of the left side are wellpreserved, whilst substantially less is preserved, or at least exposed, on the right - chiefly the ventral part of the maxilla and much of the dentary. Only small, unidentifiable pieces can be seen in addition to these. This suggests that this side was exposed and that the left lower teeth may have been lost before the skull came to rest in its final position.

DESCRIPTION

The low, slender snout is straight, probably tapering gradually forwards (Figs.2, 4). No clear indication of bony contacts is preserved on the snout, however a fissure extending anteriorly from the nasopreorbital opening may represent part of the maxillary-premaxillary contact. This feature is mildly

serrate, rather than smooth as are the breaks, and is at the expected position of this contact. The upper and lower margins of the nasopreorbital opening meet in a smooth curve. The antero-ventral margin of the nasopreorbital opening is not well preserved, and the depression in the lateral face of the snout may represent the contact surface for the jugal. An anterior tongue of the jugal overlies the lateral face of the maxilla at this position in Araripesaurus santanae and Santanadactylus araripensis (WELLNHOFER, 1985), both now attributed to Anhanguera, in Anhanguera piscator (KELLNER & TOMIDA, 2000), and in Tapejara wellnhoferi (WELLNHOFER & KELLNER, 1991). If this conjecture is correct, the anterior tongue of the jugal was substantially longer than in other known pterosaurs. Because of the loss of the dorsal margin of the snout, there is no indication whether the skull bore a crest. The first two upper teeth, exposed at the broken front of the snout, are adjacent to one another and very close to the midline, unlike the more posterior teeth, suggesting that they were actually the first two teeth at the tip of the snout. If so, the premaxilla is not clearly separated from the maxilla, which is the case in other large pterosaurs (cf. BENNETT, 2001; EATON, 1910; KELLNER & TOMIDA, 2000; and the figures of Wellnhofer, 1991a). Also implied is that the snout is relatively short anterior to the nasopreorbital opening, unlike forms such as

Pteranodon, Dsungaripterus, Anhanguera,

Gallodactylus, and Pterodactylus.

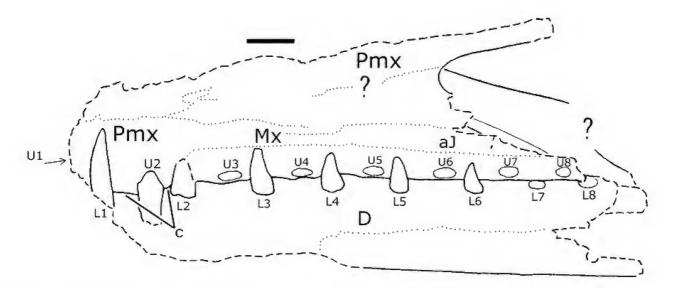


Fig.4- Outline sketch of the snout of *Mythunga camara* sp.nov. (QM F18896) indicating the extent of breakage along the margins of specimen (dashed lines). Abbreviations: (D) dentary; (Mx) maxilla; (Pmx) premaxilla; (aJ) possible articular region for jugal; (c) low collar around the second upper tooth; (U1-8) upper teeth or alveoli; (L1-8) lower teeth or alveoli. U1 indicates the position of the first upper tooth, not visible in lateral view. Scale bar = 2cm.

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The mandibular rami appear to have been straight, with dorsal and ventral margins parallel in lateral view. Unfortunately, the ventral surface of the symphyseal region has also been lost, so the presence of a mandibular 'crest' cannot be determined. Owing to the loss of the tip of the jaws, the length of the mandibular symphysis also cannot be determined. The dentigerous margins of both jaws are strongly corrugated, or scalloped, permitting deep interlocking of the upper and lower teeth. That of the upper jaw margin is straight, but descends slightly to form a low conical 'collar', overhanging the lower jaw, around the neck of the first complete tooth. The upper margin of the lower jaw is also straight.

A large, thin walled, apparently hollow element is situated in the nasopreorbital opening. It bears longitudinal grooves and ridges, and may represent the posterior part of the maxilla, or anterior part of the jugal.

Eight teeth are indicated in each jaw on the left side, and four upper and six lower on the right. These are not all visible in the text figure, as the first upper tooth of each side is exposed in the anterior break but is not visible from the side.

The anteriormost left lower tooth preserved is a crown from which the outer bone of the jaw has been broken away: it and the following tooth are about 10% larger (in diameter) than the remainder, as is the anteriormost complete upper tooth (Tab.1). Where reasonably well-preserved, the lowers seem to be smooth near the tip, but bear irregular, longitudinal striae from the neck to about two-thirds the height of the crown. The lower teeth (and the single upper) are conical and slightly recurved, but more strongly flexed in the frontal plane. The depth of the dentary is about twice the height of the preserved dentary teeth. The upper alveoli are widely spaced, but the interval between them decreases, with but a single minor exception, towards the back (Tab.2). The lower teeth seem to gradually decrease in height posteriorly. Both tooth rows have at least three teeth under the anterior region of the nasopreorbital opening and there are two dentary and two upper teeth between the mandibular symphysis and the anterior end of the nasopreorbital opening on the left. The right side shows at least four mandibular alveoli behind the posterior margin of the symphysis, and one left dentary tooth is level with the margin.

ONTOGENETIC AGE

If our interpretation of an exposed maxillary contact surface for the jugal and of a partially open suture between the maxilla and premaxilla is correct, then this skull derives from immature individual (BENNETT, 1993; 2001). The unidentified element preserved in the nasopreorbital opening may have been an element not yet fused to the rest of the skull or mandible, rather than a piece broken free. But since neither end of the piece is preserved, this cannot be determined. The symphyseal region of the mandible is very poorly preserved, but there is no indication that the symphysis was not fused. However, the preservation of the specimen is such that our interpretation of the maxillary depression and the upper break anterior to the nasopreorbital opening might be incorrect, and this represents a mature specimen.

TABLE 1. Antero-posterior diameter of left teeth at base (mm).

NUMBER	2	3	4	5	6	7	8	9
Upper	112	90 ¹	861	791	73 ¹	63 ¹	-	-
Lower	105	94	95	96	84	75	591	531

¹ Measurement of antero-posterior alveolar diameter.

TABLE 2. Spacing of teeth (on left side, mm).

INTERVAL	2-3	3-4	4-5	5-6	6-7	7-8
Upper	35	31	29	30	25	21
Lower	32	31	30	29	25	20

COMPARISON

The most recent and complete phylogenetic analyses are those of Kellner (2003) and Unwin (2003). Kellner observed that incompleteness of material (or of preparation) is a major difficulty in understanding pterosaurian relationships: of the 40 characters that he uses pertaining to the cranial skeleton, only 12 can be assessed (or estimated) for Mythunga camara sp.nov. These characters are: 3, rostral part of skull anterior to the external naris reduced vs. elongate; 6, position of the external naris above the premaxillary tooth row vs. displaced posterior to the premaxillary tooth row; 8, naris and antorbital fenestra separated vs. confluent; 13, tip of the premaxilla expanded vs. not expanded; 30, mandibular symphysis absent or very short vs. present and at least 30% of mandibular length; 34, position and presence of teeth and distribution along the jaw; 35, largest maxillary tooth positioned posteriorly vs. not so positioned; 36, variation in the size of the anterior teeth with the 5th and 6th smaller than the 4th and 7th vs. lacking this; 37, teeth with a broad and oval base vs. lacking such; 38, multicusped teeth vs. no such teeth; 39, peg-like teeth vs. no such teeth; 40, long, slender teeth vs. no such teeth. Characters 3, 8, and 39 actually have three states, but only those given here are discernible for *M. camara* sp.nov.

In *M. camara* sp.nov. the snout clearly extends well anterior of the nasopreorbital opening and that opening is apparently posterior to the premaxillary toothrow, so indicating that this taxon does not pertain to Anurognathus or an asiaticognathid. The confluent nasopreorbital opening implies reference to pterodactyloids. If, as proposed above, the first two upper teeth mark the front of the snout, there is no indication that the tip was expanded. This rules out assignment to the anhanguerids. The mandibular symphysis is clearly neither absent nor very short, indicating assignment to rhamphorhynchids or pterodactyloids. The teeth are evenly distributed along the jaws, thus eliminating reference to dsungaripterids (in which teeth are absent from the front of the jaws) or gallodactylids (in which teeth are restricted to the front of the jaws). Likewise, it could not be referred to Pteranodon, azhdarchoids, or nyctosaurids which are edentulous. The largest upper tooth (as determined from the diameter of the base or alveolus) is anterior and not positioned posteriorly thus also eliminating reference to the dsungaripterids. The 5^{th} and 6^{th} teeth are not smaller than the 4th and 7th, thus precluding assignment to Anhanguera. The remaining four characters concern unusual tooth forms characteristic of specific pterosaurian taxa. None of these occur in *Mythunga* gen.nov., and thus reference to *Peteinosaurus* or *Eudimorphodon rosenfeldi*, dsungaripterids, ctenochasmatids, *Pterodactylus antiquus*, *P. kochi* or *Germanodactylus* is ruled out.

Kellner's analysis suggests that *Mythunga* gen.nov. represents a rhamphorhynchid, plesiomorphic archaeopterodactyloid, or advanced pteranodontoid other than an anhanguerid. Confluent naris and preorbital fenestra is a character of pterodactyloids (KELLNER, 2003), so we may eliminate rhamphorhynchids. Kellner mentions only two taxa of pteranodontoids other than *Pteranodon* and anhanguerids, Istiodactylus and Ornithocheirus. The cranial material of Istiodactylus latidens is incomplete, but indicates a low, broad snout, somewhat dorso-ventrally compressed, with closely-spaced teeth (Howse et al., 2001). UNWIN (2001) has recently restudied Ornithocheirus, synonymising it with Criorhynchus, and attributing the much of material previously considered Ornithocheirus to Lonchodectes and Anhanguera. Like that of *I. latidens*, the skull of *Lonchodectes* compressirostris is fragmentary. However, the snout is clearly low, with more closely-spaced teeth than in Mythunga camara sp.nov. (OWEN, 1884). Thus *Mythunga* gen.nov. shows no significant similarities to either Istiodactylus or Lonchodectes. Ornithocheirus simus, the type species, is known from fragments of rostral and mandibular symphyses (UNWIN, 2001). In the specimen figured (CAMSM B54.428) by UNWIN (2001), the third and fourth upper alveoli are larger than the second, unlike the condition in Mythunga gen.nov.. Ornithocheirus mesembrinus had a longer rostrum anterior to the nasopreorbital aperture relative to its depth at the anterior termination of that aperture than appears to have been the case in M. camara sp.nov. with ten teeth anterior to the nasopreorbital aperture, and the third upper tooth appears to have been the largest (WELLNHOFER, 1987, Fig.2). Thus, taking into account the fragmentary nature of the material of M. camara sp.nov. (and of O. simus), we see no significant similarity between Mythunga gen.nov. and Ornithocheirus. Therefore, we provisionally regard *M. camara* sp.nov. as an archaeopterodactyloid. If the elongate depression of the maxilla does represent the contact surface for the jugal, then the anterior jugal tongue was substantially longer than in any other known pterosaur, and would constitute a third autapomorphy of M. camara.

Until recently, archaeopterodactyloids were not known from the Early Cretaceous, but they have now been found from Lower Cretaceous deposits in Liaoning, China (WANG & LÜ, 2001).

UNWIN's (2003) analysis uses 29 characters of the cranial skeleton, of which only six (17, 19, 24, 43, 55, and 57) are determinable or plausibly inferable. Of these, a bony mandibular symphysis is clearly present (character 17), teeth are present (43), dsungaripterid teeth (as defined by UNWIN, 2003) are absent, and the largest teeth are rostral (57). The naris and antorbital opening seem to be confluent (24), and if we have properly interpreted the front of the snout, the first two mandibular teeth are larger than the more posterior teeth (character 19). However, the crown of the second is incomplete, and these teeth do not seem as large relative to the more posterior crowns as in, for example, Eudimorphodon ranzii. Thus, we provisionally regard Mythunga camara sp.nov. as lacking two large fanglike anterior dentary teeth. If we are wrong, the presence of such teeth is a plesiomorphic state and so does not affect the phylogenetic assessment. These comparisons indicate that the snout derives from a breviguartossan, and plausibly a pterodactyloid, pterosaur, thus agreeing with the results from Kellner's analysis in so far as such agreement is possible given the different bases of the two analyses.

The jaws are also hollow. The medial wall of the left at its posterior break is 2.2mm thick, and the lateral wall is 1.4mm thick near the alveolar margin, and 0.9mm further ventrad. Thus the jaws seem to be essentially hollow tubes, reinforced by very thin internal partitions and struts.

The internal structure of the snout is similar to that illustrated by DALLA VECCHIA (1993) for ?Cearadactylus ligabuei, but is more regular in form. In ?C. ligabuei the chambers were seen only as a single 'layer' between the internal and external sheets of compacta. On the other hand, the structure of *M. camara* sp.nov. seems unlike that of Tupuxuara leonardii, figured by KELLNER & CAMPOS (1994). There is no indication of a transverse bony sheet as shown in their figure 7, instead the sheet is horizontal. Admittedly in *Mythunga camara* sp.nov. only the dorsal portion of the snout is available for examination, and in T. leonardii the dorsal part of the transverse sheet is quite open with large perforations, however the obvious transverse structures in the snout of Mythunga camara sp.nov.are rods or struts. Thus there are at least two different kinds of internal structure in pterosaur snouts, one shown by Mythunga camara sp.nov. and ?C. ligabuei, and the other by T. leonardii. The suspicion of Kellner & CAMPOS, that the bones of pterosaur skulls were subdivided into hollow internal chambers, is very likely correct.

INTERNAL STRUCTURE

The internal structure of the snout is exposed anteriorly. The snout is hollow with two longitudinal series of roughly rectangular chambers, 3-5mm long and 4mm wide, separated from one another by struts (Fig.5). Where clearly exposed, the chambers seem floored by a continuous, very thin sheet of bone. The floor of the anteriormost chamber (partially) exposed, however, is penetrated by roughly circular apertures, as are the roofs of the posteriormost chambers visible. Thus the structure of this part of the snout is like a series of adjacent cubic boxes. The lateral surface of the snout at this level is about 0.8mm thick but ventrally, near the alveoli, it is 1.1mm thick, presumably to withstand stresses imposed in biting.



Fig.5- *Mythunga camara* sp.nov. (QM F18896), internal structure of the snout, dorsal view. Anterior is to the right.

PADIAN *et al.* (1992) characterise pterosaurs as 'optical illusions' in that the size of their skeletal elements does not reflect the mass or weight of these elements, an 'illusion' shared with the skulls of toucans. Although the skull is mentioned in this context, their analyses (e.g., VAN DER MEULEN *et al.*, 1992) are restricted to appendicular bones. This specimen, and those of DALLA VECCHIA (1993) and KELLNER & CAMPOS (1994), indicate that the pterosaur skull and mandible were basically composed of hollow boxes and tubes, and suggests that the characterisation of the cranial skeleton as an 'optical illusion' in this sense is quite apt.

WINGSPAN

Besides its intrinsic interest, size has significant palaeoecological implications. In view of the similarities in size and general form, we have chosen to compare the skull of Mythunga camara sp.nov. with that of Anhanguera santanae (AMNH 22555) in order to estimate the wingspan of *M. camara* sp.nov. Wellnhofer (1991c) estimated the wingspan of A. santanae (AMNH 22555) as 4.15m. The only cranial measurement that can be confidently compared is that of the depth of the skull (not including the crest, if present) at the anterior end of the nasopreorbital fenestra, and even this is not entirely reliable because of the incompleteness of the dorsal margin of the snout of M. camara sp.nov. However, the general proportions of the *M. camara* sp.nov. snout suggest that not much of the dorsal region is missing, and any error resulting from this would serve to underestimate the wingspan, and so err on the side of conservatism. From Wellnhofer (1991c) we find that the depth of the snout of A. santanae at this point is about 5cm: that of the *M. camara* sp.nov. snout is 5.7cm. Thus we estimate a wingspan of approximately 4.7m. This is twice as large as the pterosaur reported by MOLNAR & THULBORN (1980), but about the size of the Western Australian specimen (BENNETT & LONG, 1991) and that represented by the pubis (QM F27104) from near Boulia.

If our interpretation of unfused bony contacts in the skull is correct, it implies that the adults of this form were somewhat larger than here estimated.

DISCUSSION

Mythunga camara sp.nov. is plesiomorphic for a Cretaceous pterosaur, e.g., it is not edentulous nor does it have a deep or curved snout. The well-developed, interlocking teeth – together with its occurrence in a

marine unit –, suggest that it preyed on fish (cf. WELLNHOFER, 1991a), and the relatively wide spacing of the teeth suggests that relatively large fish were taken.

In view of the recent publications of phylogenetic analyses of the Pterosauria (Kellner, 2003; Unwin, 2003), it is appropriate to re-assess the taxonomic affinities of the previously described postcranial material. Initially the pterosaur material from Queensland was attributed, tentatively, to the Ornithocheiridae as aff. Ornithocheirus sp. (MOLNAR & THULBORN, 1980). MOLNAR (1987) pointed out the similarities of the pterosaur pelvis from the Toolebuc to that of Pteranodon. WELLNHOFER (1991a) followed these comments and attributed the jaw fragment to *?Ornithocheirus* and the scapulocoracoid and pelvis to an indeterminate pteranodontid. Thus it was suggested in the literature that two families were represented. The recently discovered pubis (QM F27104) (Fig.6), although twice as large as that of the described partial pelvis (OM F12982), closely resembles it and so probably derives from the same taxon. The metacarpal (NMV P197962) has not yet been studied.



Fig.6- Pterosaur. Elizabeth Springs, Queensland, Australia; Toolebuc Fm., Early Cretaceous; QM F27104, pubis in right lateral view. Scale bar = 2mm. Scale in mm.

The Toolebuc scapulocoracoid (QM F10613) derives from a mature individual (BENNETT, 1993), and matches both those of Anhanguera (WELLNHOFER, 1991b, 1991c) and Pteranodon (EATON, 1910) in possessing a posterior process and a 'bridge' between the scapula and coracoid internal to the glenoid region. It further resembles that of Anhanguera santanae in the general form of the glenoid, and the V-shaped fossa on the dorso-lateral surface of the scapula between the posterior process and the anterior moiety of the scapula. Pteranodon seems to lack these features (BENNETT, 2001). KELLNER (2003) used three characters of the shoulder girdle that can be assessed for QM F10613. The proximal (glenoid) articular face of the scapula is suboval in form, rather than elongate as in more plesiomorphic taxa. This is a character state of the pteranodontoids. The scapular shaft is relatively stout and slightly constricted. This indicates membership among the pteranodontoids advanced (including anhanguerids). The scapula is substantially shorter than the coracoid, with a ratio of scapular to coracoid length of about 0.8. This is an autapomorphy of Anhanguera (Kellner, 2003). Unwin's (2003) analysis used only two characters applicable to QM F10613, that the coracoid length is greater than 75% of the scapular length (which only indicates that it pertains to a pterosaur) and that the length of the coracoid is greater than that of the scapula. This indicates that QM F10613 derived from an ornithocheiroid pterosaur. This is consistent with the results from Kellner's analysis, as Anhanguera is included in the ornithocheiroids. It thus seems reasonable to suggest that this scapulocoracoid derives from an anhanguerid that may be designated aff. Anhanguera sp.

The pubis is separated from the ischium by a deep cleft in Anhanguera santanae (WELLNHOFER, 1991b) and an apparently much less prominent one in the Toolebuc pelvis (MOLNAR, 1987), whereas in Pteranodon they are fused along their entire contact (EATON, 1910). BENNETT (1993; 1995) argued that this cleft disappears with maturity. That of the Toolebuc pelvis would fall between those of parts 2 and 3 of figure 6 of BENNETT (1995), indicating that the pelvis derived from a nearly mature individual. Because neither Kellner (2003) nor UNWIN (2003) found pelvic characters useful in analysis, we cannot be certain if apomorphic or plesiomorphic features are involved here (although because the ancestors of pterosaurs almost certainly did not show such fusion of the pubis and ischium, it is probably plesiomorphic). The mandible from near Boulia,

attributed to Ornithocheirus, now to Lonchodectes (UNWIN, 2001) and so may now be designated aff. Lonchodectes sp. UNWIN (2001; 2003) considered Lonchodectes not closely related to Ornithocheirus, but more closely related to Pterodactylus, a member of KellNER's (2003) Archaeopterodactyloidea, but distinct at the familial level.

however, closely resembles those previously

Thus, we conclude that as many as three taxa may be represented: an anhanguerid, represented by the scapulocoracoid, *Lonchodectes* or a closely related form, represented by the Boulia mandible, and *Mythunga camara* sp.nov.

ACKNOWLEDGMENTS

Phillip Gilmore found the specimen and thoughtfully donated it to the Queensland Museum. Alexander G. Cook, Alexander W. A. Kellner, Wann Langston, Jr., David M. Unwin, the late Mary Wade, and Rupert Wild kindly provided assistance during the preparation of the manuscript. Laurie Beirne first recognised the specimen as a pterosaur, and the preparation was diligently carried out by Angela Hatch. S. Christopher Bennett and an anonymous referee provided helpful comments, and Tracy L. Ford and Oliver Hampe kindly assisted in obtaining literature.

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